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SHORTER ARTICLES AND DISCUSSION

ADDITIONAL EVIDENCE OF MUTATION IN *ÆNOTHERA*

IN a group of recent papers Bartlett reports on the remarkable behavior of certain wild species of *Ænothera* grown in large cultures, which behavior he regards as strong evidence for the mutation theory of De Vries. The facts are presented very clearly, but there is, however, a point of view which has not been considered in the interpretation of the conditions in his material, certain possibilities that must be reckoned with in the critical examination of such evidence. The suggestions that I shall offer will concern chiefly the genetic purity of the forms studied, a condition which is of course basic to studies on mutation as well as to Mendelian experimentation.

Ænothera pratincola Bartlett¹ is a small-flowered, close-pollinated species apparently common in the North Central States. Seven strains derived from wild mother plants at Lexington, Kentucky, gave rise to a variant, *nummularia*, which differs from the parent type in the form of the seedling leaves, foliage, pubescence of the ovary and calyx, and in the manner in which the calyx is ruptured in the opening of the flower. *Nummularia* appeared with a frequency of about 1 plant to every 400 seeds sown and 1 plant to every 250 seedlings since the germination of the seeds in the earth was 66 per cent. Two of the strains produced *nummularia* in both the F_1 and F_2 generations. Further studies will be undertaken to determine whether *pratincola* will continue to give *nummularia* or whether it may perhaps in later generations produce stable individuals. *Nummularia* develops a low percentage of good pollen (less than 50 per cent.) while *pratincola* has a high proportion (90 per cent.); *nummularia* also forms very few good seeds to a capsule, and of these only 34 per cent. are viable. Small cultures grown from *nummularia* seeds gave no plants of *pratincola*, but certain new forms appeared. The high degree of sterility both gametic and zygotic shown by *nummularia* is striking and demands study, for it will make a difference in the interpretation of the behavior of this plant whether the sterility is physiological or genetic in character.

¹ Bartlett, H. H., "Additional Evidence of Mutation in *Ænothera*," *Bot. Gaz.*, Vol. LIX, p. 81, 1915.

Cultures of *pratincola* and *nummularia* should be grown from germinations established experimentally to be complete, with records of the residue of sterile seed-like structures, and the two forms should be crossed with the purest *Oenothera* known to determine whether or not the F_1 hybrid generations are uniform. Should F_1 hybrid generations consist of distinct classes we would be justly suspicious of the purity of the stock.

A second paper of Bartlett² describes a series of cultures of *Oenothera stenomeræ*, a cruciate-flowered species from Montgomery County, Maryland. Two sharply marked new types were produced by the typical form of the species, *gigas* represented by one specimen with 28 chromosomes, and *lasiopetala* with hairy petals. The *gigas* plant appeared in the F_4 generation of a line of *stenomeræ*. The peculiarities separating it from *stenomeræ* are similar to the distinctions between *Lamarckiana* and its derivative *gigas*. Thus both *gigas* forms are more persistently biennial in habit than their parents, both have thicker, broader leaves, stouter stems, larger buds, thicker fruits, 4-lobed pollen grains, and twice as many chromosomes. A progeny of 63 individuals from the original *gigas* plant consisted of 54 typical *gigas*, 6 narrow-leaved variants, and 3 "secondary mutations"; the form thus, as with the *gigas* from *Lamarckiana*, produces a varied offspring. Two of the "secondary mutations" were dwarfs and one had the characters of *lasiopetala*, hairy petals, and in addition certain of the stamens were also hairy.

Lasiopetala was noted in an F_3 generation and also in two cultures of an F_4 ; it is of infrequent occurrence, only 5 plants in all being observed. The plants formed persistent rosettes (*stenomeræ* being annual) and only one branch produced flowers, these with hairy petals. The pollen of *lasiopetala* is 40–50 per cent. perfect; that of *stenomeræ* 60–80 per cent. An F_1 progeny of 116 plants from selfed *lasiopetala* gave 60 per cent. typical *stenomeræ* and 40 per cent. *lasiopetala*, thus behaving like *Oenothera lata* and *O. scintillans* in throwing their parent form *Lamarckiana*.

Of these two new types derived from *O. stenomeræ* the *gigas* plant is remarkable as being another of the very few *œnothæras* discovered with the quadruploid number of chromosomes (28); triploid forms usually named *semigigas* have been described from a number of lines. The hairiness of the petals in *lasiopetala* is

² Bartlett, H. H., "The Mutations of *Oenothera stenomeræ*," *Amer. Jour. Bot.*, Vol. II, p. 100, 1915.

regarded by Bartlett as a character new to the genus. Bartlett emphasizes the fact that the characters of neither type could be interpreted as the result of segregation following hybridization, which may be true, but I do not think from this that it follows that neither type can be the result of hybridization. I am not willing to admit that hybrids present only combinations of characters derived from their parent lines. It seems to me reasonable to believe that in hybrids at times the interaction of elements modifies the old or produces new factors. The species *stenomeres* and the derivatives *gigas* and *lasiopetala* have not been tested for genetic purity by cross-breeding with relatively stable types and the problems of gametic and zygotic sterility have not yet been attacked.

The final paper of this group of Bartlett's³ deals with an extremely interesting situation developed in cultures of *Ænothera Reynoldsii* from Knoxville, Tennessee. This is also a small-flowered, close-pollinated species, and its peculiarity lies in an ability to throw extraordinarily large classes of dwarfs. There are two types of dwarfs: (1) *semialta* somewhat smaller than the typical *Reynoldsii* and intermediate between it and the smaller dwarf; (2) *debilis*. A plant of *Reynoldsii* in the F₃ produced 29 individuals like itself, 32 plants of *semialta*, and 18 of *debilis*, i. e., 60 per cent. of its offspring were dwarfs. *Semialta* throws *debilis*, but no *Reynoldsii*. *Debilis* apparently can produce no *Reynoldsii* or *semialta* and breeds true except for an occasional variant *bilonga* which was also found in one culture from typical *Reynoldsii*.

With respect to the dwarfs we have here presented a beautiful series leading from the unstable parent type *Reynoldsii* through the more stable *semialta* to the most stable and most extreme dwarf *debilis*. Bartlett calls the behavior mutation *en masse*, but confesses that it bears a certain degree of resemblance to Mendelian segregation. We should very much like to see this study repeated on a larger scale and with experimental germination of the seed so that we may be sure of the ratios and also certain that the cultures have given us all of their possible progeny. Segregation *en masse* seems to the writer likely to be a more probable explanation of the phenomena than mutation.

The form *bilonga* derived from the dwarf *debilis* offers a particularly interesting problem. It is similar to *semialta* except that

³ Bartlett, H. H., "Mutation *en masse*," AMER. NAT., Vol. XLIX, p. 129, 1915.

the fruits are twice as long. The capsules sometimes reach the length of 70 mm. and average above 60 mm.; they are very much the longest fruits reported in the subgenus *Onagra*. Bartlett regards this large size of capsule as the origin of a new character. Now capsule size obviously depends upon the number of ovules produced which develop into seeds. It thus becomes an important matter to obtain the data on ovule sterility in the species *Reynoldsii* and the derived forms *semialta*, *debilis* and *bilonga*. Ovule sterility is widespread among the *Oenotheras* as all students of the genus know. Should it be found that *bilonga* produces a very much greater number of ovules than *debilis* and the other types this fact would indicate a true progressive advance. It may, however, be found that the smaller size of the capsules of *Reynoldsii semialta*, and *debilis* is due to ovule sterility, *i. e.*, to the inability of a large proportion of the ovules to set seed. This would point to a very different interpretation of the conditions in *bilonga*, and might indicate that *bilonga* is an example of reversion towards an ancestral type in which a large capsule was correlated with a high degree of ovule fertility.

In the comments which I have presented on the extremely interesting facts discovered by Bartlett no attempts have been made to offer exact explanations in line with Mendelian analysis. It is not difficult to spin hypotheses on assumptions which have been neither established nor disproved, but such creations are hardly worth the effort when the facts are within grasp. My main point is a constant questioning of the genetic purity of the material with which Bartlett has worked from the standpoint developed in my forthcoming paper "The Test of a Pure Species of *Oenothera*."⁴ It is impossible to discuss this subject in the short space of a review. The most important test is that of cross-breeding with the purest species known, to judge from the uniformity of the F_1 hybrid generation whether or not the parent types are pure. I also firmly believe that all exact genetical work on *oenotheras* must make use of methods of experimental germination to ensure complete progenies from the viable seeds and to permit the preservation of a residue of ungerminated structures that may be examined.⁵ There is in addition the determination

⁴ To appear in the *Proceedings of the American Philosophical Society*, Vol. LIV, 1915.

⁵ Davis, B. M., "A Method of Obtaining Complete Germination of Seeds in *Oenothera* and of Recording the Residue of Sterile Seed-like Structures," *Proc. Nat. Acad. Sci.*, Vol. I, p. 360, 1915.

of degrees of sterility both gametic and zygotic, and the consideration of whether such sterility is genetic or physiological. From such tests it is possible to reach much clearer conclusions on the genetic purity of *Oenothera* material than has been possible in the past.

Finally reference should be made to the important confirmation by De Vries⁶ of the studies of Stomps on *Oenothera biennis* L. In large cultures totaling 8,500 plants from Stomps's selfed line De Vries obtained 8 plants of a dwarf *biennis nanella* about 0.1 per cent., 4 plants of *biennis semigigas* (21 chromosomes) about 0.05 per cent., and 27 plants of the color variety *biennis sulfurea* about 0.3 per cent. Since the percentages from *Lamarckiana* are for *nanella* 1-2 per cent. and for *semigigas* 3 per cent., it would appear that *biennis* is the more stable of the two species, although the color variety *biennis sulfurea* is a new type in experimental studies in *Oenothera*. A culture of over 1,000 plants from selfed seed of *biennis sulfurea*, all with pale yellow flowers, produced 2 dwarfs, thus giving what De Vries calls a "double mutant," *O. biennis* mut. *sulfurea* mut. *nanella*.

This behavior of *Oenothera biennis* is to the writer much more trustworthy evidence for mutation than that presented from the studies on *Lamarckiana* since *biennis* has a record of a long history as a species on the sand hills of Holland, where there appears to have been little probability of recent contamination. However, the showing of "mutants" from *biennis* does not appear very encouraging for the mutation theory of organic evolution when it is remembered that *biennis nanella* is frequently weakly or diseased, that *biennis semigigas* is self sterile, and that *biennis sulfurea* appears to be a retrogressive form having lost the power of producing normal yellow flowers. Although the Dutch *biennis* of all the *oenotheras* so far brought into the experimental garden still seems to me the form most free from suspicion of genetic impurity, nevertheless, the line of Stomps's has not, so far as we know, been subjected to all of the tests of a pure species. Until these tests are made it is not safe to assume that this material is wholly pure. It seems to me not improbable that other species of *Oenothera* will eventually be isolated more stable than the Dutch *biennis*.

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⁶ De Vries, Hugo, "The Coefficient of Mutation in *Oenothera biennis* L.," *Bot. Gaz.*, Vol. LIX, p. 169, 1915.